THE FLORA OF NORWAY AND ITS IMMIGRATION

N. WILLE

Professor at the Christiania University

The phytogeographical investigations in a country may be carried on in the following three main directions:

Floristic phytogeography, or an investigation into the geographical distribution of the plant species. The result of this work should be charts of the distribution in the country of the various species. In a country with such varied conditions of life as Norway, this is a very comprehensive and very arduous task, requiring an infinitude of detailed investigations in all parts of the country.

Ecological phytogeography, which endeavors to find out how and why the different species of plants in various places and under various conditions of life come together in plant-communities. This branch of science, which was founded by Professor E. Warming, must be based upon phytoanatomy and phytophysiology, as the connection between the organization of the vegetable species and their external conditions of life must be investigated. Investigations such as these may yield interesting results in all countries, and are most easily carried on where the conditions of life are uniform over wide areas; but in a country like Norway, with its varied conditions, they present very great difficulties.

Historical phytogeography has for its aim the investigation of the changes that in the course of time have taken place in the vegetation of a country—to find out, for instance, when and whence important species have immigrated, how quickly they have spread, why others, that had formerly been more widely distributed, had a more restricted distribution in a later period, etc., etc.

With regard to this last branch of science, the Scandinavian countries, Denmark, Finland, Norway, and Sweden, present peculiarly favorable conditions; for there is no doubt that these countries were formerly buried under a continu-

ous covering of ice, which destroyed all vegetation except perhaps the most hardy. All other species of plants have immigrated subsequently from the neighboring countries, which were not covered with ice during the Glacial Epoch, and could therefore afford a dwelling-place for a more or less abundant flora.

In the following pages I shall endeavor to give an account of the results at which historical phytogeography may be said to have arrived as far as Norway is concerned.

Survey of the Distribution of the Norwegian Flora

It will first be necessary, however, to give a general account of the most important points regarding the composition and distribution of the Norwegian flora throughout the country. I shall here consider only the vascular plants (about 1,500 species), however, as the distribution of the lower plants is not sufficiently known to enable us to draw definite conclusions.

The area of Norway is about 125,000 square miles, stretching from latitude 57° 58′ 43″ north to latitude 71° 10′ 20″ north. The conditions for plant life will thus be very different in the southern and northern parts of the country. But in addition to this, there is a great difference between the climate in the east and that in the west of southern Norway. In the valleys of the East Country, there is a very pronounced inland climate, with hot summers and a winter temperature that falls below —40° C., while on the west coast region there is a low summer temperature, but a mean January temperature of sometimes more than 2° C.

The most important condition affecting the distribution of plants in Norway is the temperature. In this connection we shall in the first place speak of the lowest winter temperature that the plants can survive. J. Holmboe ('13) has shown that the distribution of *Ilex aquifolium* in Norway coincides closely with the January isotherm for 0° C. Herbaceous plants which die down in the winter may of course be independent of the lowest winter temperature, as they are covered with snow; but they are not entirely independent of

the spring and autumn temperature. Plants are also in a great measure dependent on the height of the temperature in the period of vegetation, which, in Norway, comprises in the main the four months, June, July, August, and September.

Fig. 1. Isotherms for January.

In this way, the conditions prevailing in Norway are very varied, the July isotherm for Christiania being 17°C., while for the west coast it is only from 12 to 14°C.

A. Helland ('12) has calculated that where the mean summer temperature in Norway is less than 13°C., the fruit

trees yield nothing worth mentioning; and where it is less than 11° C., the cultivation of grain is uncertain. The minimum limits of the necessary mean summer heat for the following wild Norwegian trees and shrubs appears to be as

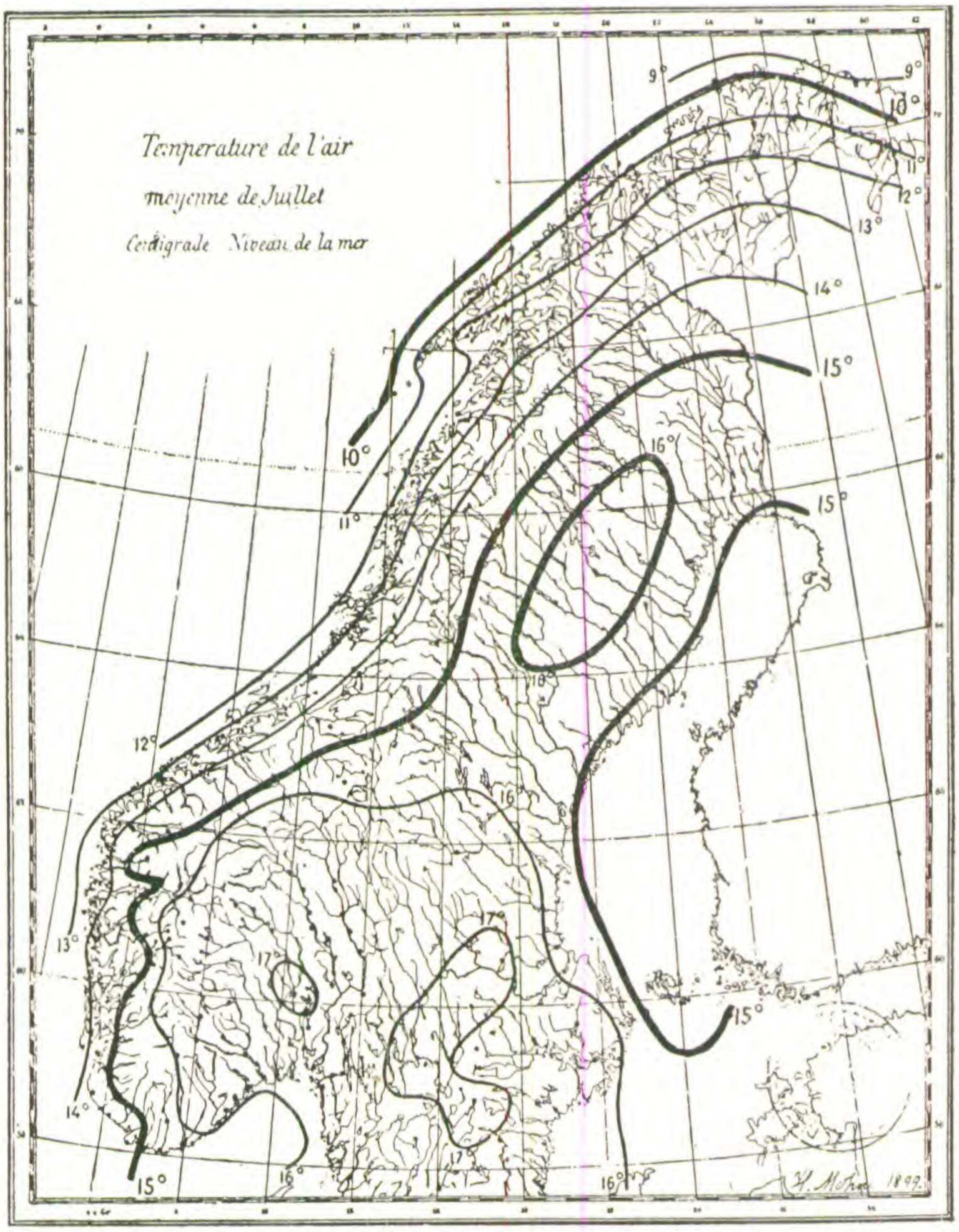

Fig. 2. Isotherms for July.

follows: for *Fagus sylvatica,* 13.4° C.; *Quercus pedunculata,* 12.6° C.; *Corylus Avellana, Acer platanoides,* and *Tilia cordata,* 12.5° C.; *Alnus glutinosa* and *Fraxinus excelsior,* 12.4° C.; *Sorbus Aria* and *Ulmus montana,* 11.2° C.; *Picea excelsa* and *Pinus sylvestris,* 8.4° C.; *Alnus incana, Prunus Padus,*

and *Sorbus Aucuparia,* 7.7°C.; *Populus tremula,* 7.6°C.; *Betula odorata,* 7.5°C.; *Juniperus communis* var. *nana,* 5.3° C.; and *Betula nana,* 4.3°C.

As the mean temperature of summer decreases with increasing height above sea-level very nearly 0.6°C. per 330 feet, the distribution of plants is greatly influenced by the circumstance that Norway is a mountainous country, its highest mountain, Galdhöpiggen, being 8,095 feet in height, and thus within the region of perpetual snow. But a peculiarity of the Norwegian mountains is that they form broad (as much as sixty-two miles broad), undulating mountain plateaus, which are intersected by deep or shallow valleys, where there are narrow lakes or small rivers. The edge of these mountain plateaus, in the south of Norway, lies at a height of from 2,950 to 3,280 feet above the sea, so that *Picea excelsa* and *Pinus sylvestris* disappear slightly below this height, the edge of the plateaus and the lowest valleys that intersect them being covered with *Betula odorata.* The great mass of the mountain plateaus, which rise above the birch-limit, is thus treeless.

It has been calculated that there are 26,333 square miles of forest land in Norway, of which 73 per cent consists of *Picea excelsa* and *Pinus sylvestris,* while the remaining 27 per cent is mainly *Betula odorata* with a little *Betula verrucosa, Quercus pedunculata,* and *Q. sessiliflora,* and a very little *Fagus sylvatica* in the south.

The vegetation limits are lower not only toward the north, as one would expect, but also toward the west, as they are lower near the sea than inland. This will be seen from the following height-limits in feet:

	Snow-line ft.	Birch-limit ft.	Pine-limit ft.
Gausta in Telemarken (south of Norway)	....	3450	3024-3113
Vos (west of Norway)	3936	3359	1994
Snehaetta, in the Dovre Mountains (central Norway)	5375	3464	2880
Rödö in Helgeland (just within the Arctic Circle)	3280	....	777
Alten in Finmark (70° N. Lat.)	3516	1476	777-1023

The distribution northward and height above sea-level of the various vegetable species, will be dependent mainly upon the temperature during the summer months.

The rainfall, which in various other countries plays so important a part as a factor in vegetation, is of less import-

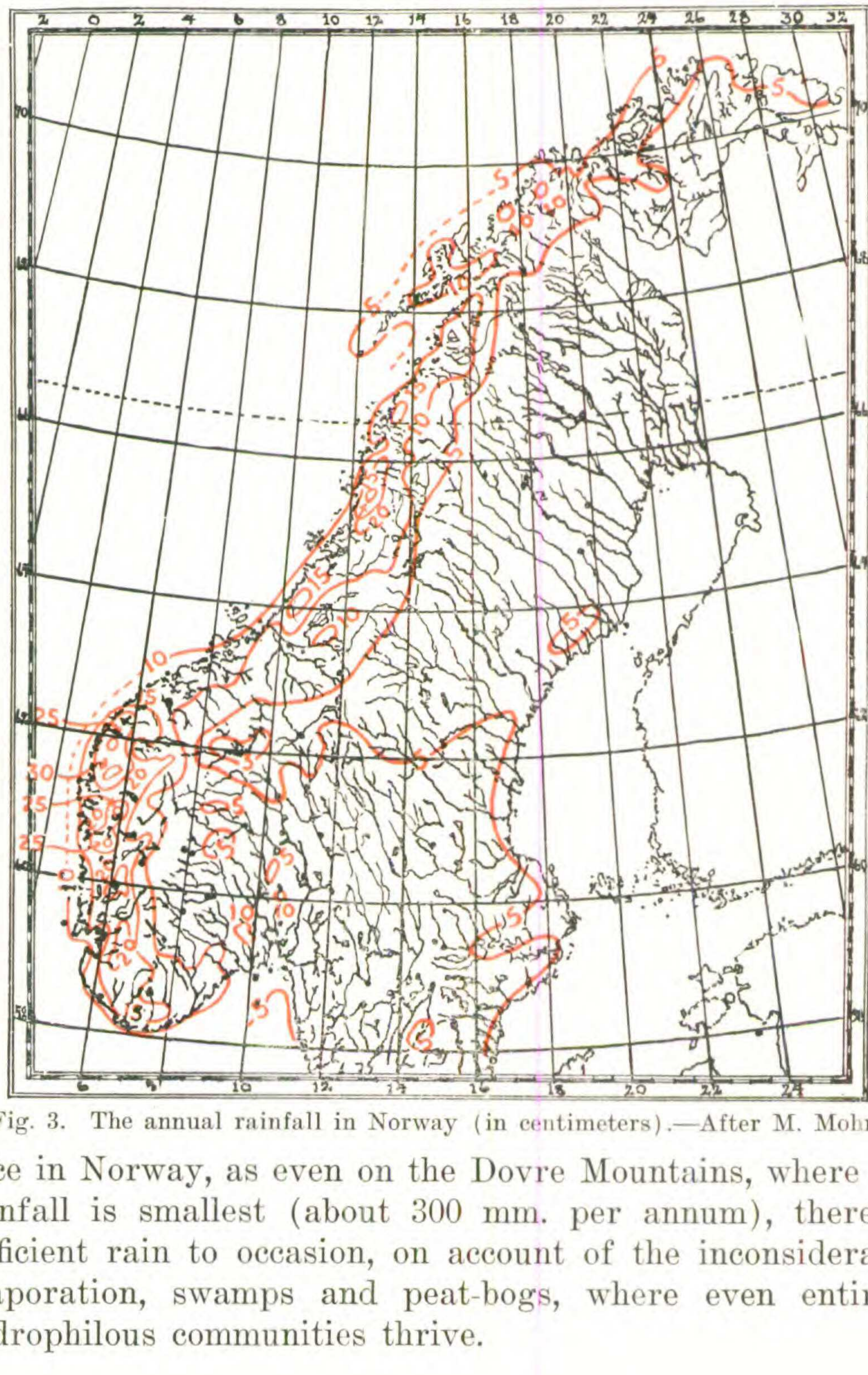

Fig. 3. The annual rainfall in Norway (in centimeters).—After M. Mohn.

ance in Norway, as even on the Dovre Mountains, where the rainfall is smallest (about 300 mm. per annum), there is sufficient rain to occasion, on account of the inconsiderable evaporation, swamps and peat-bogs, where even entirely hydrophilous communities thrive.

It was formerly supposed that the largest rainfall was on the outermost islands off the west coast of Norway, and that this was the cause of the Atlantic vegetation that is found there, with such characteristic plants as *Hymenophyllum peltatum, Erica cinerea, Scilla verna, Vicia Orobus,* etc. But more recent investigations have shown that the rainfall is greater a little way in from the coast, where the mountains begin. In Hovlandsdal, near the Sogne Fjord, a mean rainfall has been observed of 3,178 mm., and at Skaanevik, near the Folgefon, 2,945 mm., whereas the outermost islands off Bergen show a rainfall of only 1,300 mm., and off Florö of 1,900 mm. It is, therefore, clear that the occurrence of the above-mentioned Atlantic plants on the outermost islands is due not to a larger rainfall, but to a milder winter temperature.

There are, of course, species of plants that cannot thrive in the great humidity of the West Coast; but as there are also localities with comparatively dry soil, it may be rather the low summer temperature than the large rainfall that prevents them from thriving.

The importance of the soil for vegetable growth appears to depend, in Norway, mainly upon whether the soil is rich, or deficient, in lime. In addition to its chemical influence, a calcareous subsoil, especially when consisting of calcareous slate or limestone, is of consequence from the fact that it forms a warm soil. In Norway, therefore, most of the southern species are found only in the limestone country surrounding the Skien Fjord and the upper part of the Kristiania Fjord.

The terrestrial plants of Norway may be divided into five zones, according to the ability of the plants to ascend the mountains and extend northward in their growth, that is to say, according to their dependence on the mean temperature of the summer. These zones are here indicated by the upper limit of a characteristic species of plant.

I. THE QUERCUS PEDUNCULATA ZONE

In the east of Norway this tree is found as far as Lake Mjösen (60° 45′ N.), and in the west up to Nordmöre (62°

55'); but it is nowhere known to have reached a greater height above sea-level than 1,722 feet.

The oak can stand a winter temperature as low as —33.8° C., but requires a mean summer temperature of 12.6°C. It is now comparatively rare, and seems to be decreasing. It occurs in large quantities only on the Silurian and along the lower parts of the coast.

A number of deciduous trees that are susceptible to cold have about the same distribution as the oak, both in height and in northward extension. These are: *Acer platanoides, Alnus glutinosa, Betula verrucosa, Crataegus Oxyacantha, Fraxinus excelsior, Prunus avium, P. insititia, Pyrus Malus, Sorbus Aria, S. fennica, Taxus baccata,* and *Tilia cordata.* There are also a number of species of cryptogams. It may on the whole be said that the zone here designated the Oak Zone is that of Norway's most abundant flora.

Within the Oak Zone, large districts may in their turn be marked off that possess a characteristic flora, the occurrence of which is especially conditioned by circumstances of temperature and soil.

1. *The Region of the Silurian Flora.*—This is developed in an especially characteristic manner on the calcareous slate along the Langesund Fjord, the west side of the Kristiania Fjord, in Ringerike and Hadeland, and around Lake Mjösen. In some of these districts it is fairly cold in the winter, but very hot in the summer;[1] and as the soil is calcareous and warm, a xerophilous steppe-flora, with its characteristic *Labiatae, Boragineae,* and *Centaurea* species, and thistles, such as *Carlina vulgaris, Carduus acanthoides,* etc.—species which also occur in the steppe-regions of South Russia, can thrive well on southern slopes.

For the rest, the flora is rich in characteristic species, e.g., *Artemisia campestris, Brachypodium pinnatum, Carex praecox, Cephalanthera rubra, Cirsium acaule, Fragaria collina, Libanotis montana, Ononis campestris, Phleum phalaroides,*

[1] In Kristiania, the 30-years' average minimum atmospheric temperature for the month of January is —16.5°C., and the average maximum for the month of June +28.9°C.

Spiraea Filipendula, Thymus Chamaedrys, Trifolium montanum, Veronica spicata, etc.

Where the soil is deep and not too dry, the above-mentioned deciduous trees that are susceptible to cold form forests or copses, intermingled with *Corylus Avellana, Prunus spinosa,* species of *Rosa* and *Rubus,* and a luxuriant ground vegetation, among which are several orchids.

A few of these trees and the more hardy species of the Silurian flora, such as *Origanum vulgare* and others, may, like an advance-guard, overstep the boundaries of the Silurian regions, but then they generally occur in warm localities, in talus at the foot of cliffs, or in steep slopes that face southward, even high up the sides of the valleys, or in the upper parts of the West Country fjords.

But the number of species diminishes with increasing distance from the lowland Silurian regions, and there are only a few species that have advanced as far as north of the Dovre Mountains.

2. The Region of Fagus sylvatica.—This region is situated along the southeast coast of Norway, from the Swedish border to Grimstad, where it extends as far north as Holmestrand. There is a small beech-wood a little to the north of Bergen, but this is a solitary instance, and has nothing to do with the real distribution area of the beech.

The beech is purely a lowland plant, as there is only one place in which it goes to a height of 886 feet above the sea, its usual height being not more than 525 feet. When cultivated, it can grow almost as far north as *Quercus pedunculata,* but prefers a rather higher summer temperature (13.4°C.) and thrives best on comparatively warm gravel banks.

The beech is one of those plants which has recently appeared to spread to new regions; and there is no doubt that it has not yet nearly reached the limits of distribution to which it will little by little attain, especially along the low land of the south coast. This is due to the fact that it must have immigrated in fairly recent times.

The following plants may also be mentioned as occurring chiefly in the region of the beech: *Cladium Mariscus, Coron-*

illa Emerus, Epilobium obscurum, Laserpitium latifolium, Ligustrum vulgare, Luzula nemorosa, Melampyrum cristatum, Rubus corylifolius, R. Lindebergii, Selinum carvifolium, Sium latifolium, Viscum album, Vicia cassubica, V. lathyroides, etc. A few of these have a rather larger distribution than the beech has at present; others, which must have immigrated recently, are found only within quite a small area.

The region for the cultivation of wheat in Norway coincides in the main with that of the beech, but extends a little farther, namely westward as far as Mandal, and to a height of 1,246 feet above sea-level.

3. *The Region of Ilex Aquifolium.*—This region is situated a little to the west of that of the beech, and does not have a lower mean temperature for January than 1°C. It extends from Arendal to Christianssund (63° 7′ N. Lat.), but does not include the outermost islands on the west coast.

A large number of vegetable species occur in this region. As especially characteristic may be mentioned *Aeropsis praecox, Asplenium Adiantum nigrum, Cardamine hirsuta, Centaurea decipiens, C. nigra, C. pseudophrygia, Cerastium tetrandrum, Chrysosplenium oppositifolium, Circaea lutetiana, Conopodium denudatum, Corydalis claviculata, Cynosurus cristatus, Digitalis purpurea, Drosera intermedia, Gentiana Pneumonanthe, Geranium columbinum, Hedera Helix, Heracleum australe, Hydrocotyle vulgaris, Hypericum pulchrum, Hypochaeris radicata, Juncus squarrosus, Leontodon hispidus, Luzula sylvatica, Lysimachia nemorum, Meum athamanticum, Quercus sessiliflora, Pilularia globulifera, Polygala depressum, Primula acaulis, Rosa pimpinellifolia, Rumex obtusifolius, Sagina subulata, Scirpus setaceus, Sedum anglicum, Senecio Jacobaea, Stellaria Holostea, Teesdalia nudicaulis, Triticum acutum, T. junceum,* and *Weingartneria canescens.*

A few of these species, however, can bear a January isotherm that lies a little lower than 1°C. These species, among which are *Hedera Helix* and *Quercus sessiliflora,* occur, therefore, also in the beech region in the southeast of Norway, but have their chief distribution in the Ilex Region, and must therefore be assigned to that region.

4. *The Region of the West-European Coast Flora.*—This includes the outermost islands in the province of Bergen. The characteristic feature of the climatic conditions here, as we have already stated, is not the large rainfall, for this is in reality smaller than in certain parts of the Ilex Region; but it is the extremely mild winter temperature, and a comparatively low summer temperature.

For purposes of comparison we will here give the mean minima for February and the mean maxima for July, for Kristiania, which forms a center for the Silurian flora, Larvik, the center of the beech region, Mandal of the holly, and Utsire of the West-European coast flora.

	Mean minimum temperature for February	Mean maximum temperature for July
Kristiania	15.5° C.	28.8° C.
Larvik	14.5° C.	25.8° C.
Mandal	11.3° C.	24.8° C.
Utsire	5.7° C.	19.9° C.

On these outermost islands in the province of Bergen, the mean temperature for January is 2°C.

Among the plant species that are especially characteristic of this region may be mentioned *Asplenium marinum, Erica cinerea, Hymenophyllum peltatum, Scilla verna,* and *Vicia Orobus.* These species are found in England, and some of them southward along the shore of the Atlantic.

II. THE PINUS SYLVESTRIS ZONE

In the east of Norway *Pinus sylvestris* goes right down to the sea, and occurs in many places in the Oak Zone; but in speaking here of a special zone for *Pinus sylvestris,* we refer to the great continuous forests of *Pinus sylvestris* and *Picea excelsa,* which cover wide tracts of country from the upper limit of the Oak Zone to a height of 3,116 feet in the south of Norway, 1,640 in the central part, and 623 in the north. *Pinus sylvestris* avoids the sea, and is therefore absent from the outermost belt of islands; but inland it forms, either alone or together with *Picea excelsa,* a more or less continuous region of distribution below the above-stated height-limits up to latitude 70°N.

Picea excelsa, which immigrated much later than *Pinus sylvestris,* supplants the latter in favorable localities in the east of Norway; but in the west its field of distribution is very small, and extends only to latitude 69°N. Farther north, in the interior of Finmark, small spruce forests do indeed occur, but they are formed of *Picea obovata.*

The forests that are formed of *Pinus sylvestris* are light, but as they often grow upon dry, poor soil, they are poorly furnished with vegetable species. There may occur scattered specimens of *Betula odorata, Alnus incana, Juniperus communis, Sorbus Aucuparia,* and *Populus tremula,* and then a poor ground vegetation of mosses (e.g., *Polytrichum juniperinum*), and lichens (e.g., *Cladonia rangiferina, Cetraria islandica,* and *Peltigera*), among which grow some easily contented higher plants, especially *Aira flexuosa, Arctostaphylos officinalis, Calluna vulgaris, Empetrum nigrum, Festuca ovina, Luzula pilosa, Melampyrum sylvaticum, Pteris aquilina, Trientalis europaea, Vaccinium Myrtillus, V. uliginosum,* and *V. Vitis-Idaea.*

Where this forest, from some cause or other, has been destroyed, extensive heath-lands are often formed, consisting chiefly of *Calluna vulgaris,* among which occur *Empetrum nigrum* and species of *Vaccinium,* as also *Antennaria dioica, Aira flexuosa, Campanula rotundifolia, Festuca ovina, Nardus stricta,* and others.

Picea excelsa forms forests on more fertile soil; but as they are very dense and dark, other trees have difficulty in forcing an entrance, and even the ground vegetation is as a rule very poor, owing to the want of light. A thick carpet of mosses (especially *Hylocomium splendens*) covers the ground, and the only plants that thrive are fungi, *Polystichum spinulosum* and some other ferns, *Linnaea borealis, Milium effusum, Oxalis Acetosella, Pyrola uniflora,* and others.

Where the forests of *Picea* are less dense, or where *Pinus sylvestris* grows upon a more fertile soil, these conifers may be mingled with various deciduous trees, and in the lower districts even with less hardy deciduous trees, which otherwise belong to the Oak Zone. The ground vegetation in such

places is also much more abundant, and the ordinary lowland flora may be found fairly well represented.

Almost all cultivated land in Norway lies in the Oak and Pine Zones. Rye and oats ripen up to latitude 69°N., barley even up to 70°N.—in the south it can be grown up to a height of 2,066 feet above the sea. The potato is cultivated rather farther north and a little higher above sea-level than barley. Side by side with the growing of grain is that of forage plants, of which the most important species are *Trifolium pratense* and *Phleum pratense.*

III. THE BETULA ODORATA ZONE

Betula odorata also occurs in the lowlands, and extends farther toward the sea than *Pinus sylvestris,* but by its zone, as here defined, is meant the region above the height limit of *Pinus sylvestris* upon the mountains and north of its distribution. In the very south of Norway, *Betula odorata* goes up to about 3,600 feet above the sea, and northward as far as latitude 71° 10′ N. Thus beyond the Birch Zone there is only the northeastern part of Finmark and the highest mountain regions.

In the south of Norway the great proportion of the so-called "saeters" lies in the Birch Zone, as this tree generally occupies the margin of the mountain wastes, and fills the little valleys that intersect them with a short-stemmed forest of *Betula odorata* subsp. *alpigena.*

Side by side with this mountain form of birch, there may also grow *Alnus incana, Populus tremula, Prunus Padus* and *Sorbus Aucuparia.* The ground vegetation will be somewhat variable according to the degree of moisture in the soil.

On dry gravelly slopes, especially if they face the south, the following species of higher plants are generally found in addition to a few species of lichens, such as *Cetraria islandica, Stereocaulon,* etc.: *Arctostaphylos officinalis, Agrostis vulgaris, Aira flexuosa, Alchemilla alpina, A. vulgaris* var. *pubescens, Antennaria dioica, Anthoxanthum odoratum, Astragalus alpinus, Botrychium Lunaria, Betula nana, Calluna vulgaris,* some species of *Carex, Empetrum nigrum*

Euphrasia officinalis, Festuca ovina, Gnaphalium norvegicum, Juniperus communis, Lotus corniculatus, Luzula campestris, L. pilosa, Maianthemum bifolium, Melampyrum sylvaticum, Nardus stricta, Pedicularis Oederi, Peristylis viridis, Phleum alpinum, Poa alpina, Pyrola minor, Rhinanthus minor, Solidago Virgaurea, Trientalis europaea, Vaccinium Myrtillus, V. uliginosum, V. Vitis-Idaea, and *Vicia Cracca.*

Where the soil is deeper and damper, and along streams and in shady places, *Salix glauca, S. hastata, S. lanata, S. lapponum, S. Myrsinites* and their hybrids make their appearance. The vegetation here is more luxuriant, as in addition to most of the above-named, the following species are found: *Aconitum septentrionale, Agrostis rubra, Alchemilla vulgaris* var. *alpestris, Aira alpina, A. caespitosa, Bartschia alpina,* species of *Carex, Equisetum hiemale, Geranium sylvaticum, Gymnadenia conopea, Montia fontana, Mulgedium alpinum, Myosotis sylvatica, Orchis maculata, Polygonum viviparum, Pinguicula vulgaris, Polemonium caeruleum, Ranunculus platanifolius, Rumex Acetosa, Saussurea alpina, Selaginella spinulosa, Soyera paludosa, Spiraea Ulmaria, Viola biflora,* and others. Many of these species occur right down to sea-level, some also higher up in the next zone; but as they are always found in the Birch Zone and have their most abundant development there, it is best to refer them to that zone.

IV. THE ZONE OF DWARF WILLOWS

This zone occupies the northeast part of the Varanger peninsula in Finmark and the mountains above the birch limit, up to a height which, in the southernmost point, may be put at 4,133 feet above the sea. It is thus only the tops of the highest mountains which rise like islands above this zone. The mean summer temperature here will be from 8.5 to 4.3°C., according to the height and situation in higher latitudes. The composition of the vegetation varies greatly according to the moisture conditions of the soil, which in their turn to some extent depend on exposure to the sun, south slopes being dry, north slopes damp.

On the drier tracts there are low copses of *Betula nana* and *Juniperus nana,* with a ground vegetation of mosses and lichens and a poor selection of mountain plants, such as *Antennaria alpina, Arctostaphylos alpina, Azalea procumbens, Carex rigida, Hieracium alpinum, Juncus trifidus, Erigeron alpinus, E. uniflorus, Festuca ovina, Gnaphalium supinum, Luzula arcuata, Luzula nivalis, L. spicata, Lycopodium alpinum, L. Selago, Nardus stricta, Pedicularis lapponica, Polygonum viviparum, Rhodiola rosea, Salix herbacea, S. reticulata, Trientalis europaea, Vaccinium Myrtillus, V. uliginosum, V. Vitis-Idaea, Viscaria alpina,* and others.

Where the soil is very poor and the climate during the vegetation period very dry, as on the mountain moorlands in the east of Norway—'round the lake Faemundsoe, and between the valleys Oesterdal and Gudbrandsdal—there occur great lichen-covered heaths consisting of *Cladonia rangiferina, Cetraria nivalis, C. cucullata, Alectoria divergens,* and *A. nigricans,* which give a grayish white appearance to the mountains. Among the masses of lichens there are found only a few very easily satisfied mountain plants such as *Festuca ovina, Nardus stricta, Solidago Virgaurea,* etc.

Where, on the other hand, the soil abounds in lime, and the conditions otherwise are favorable, as in certain places on the Hardanger Plateau in the south, Lom and Dovre in the center, and several places in the north of Norway, rare mountain plants occur, such as *Alsine biflora, A. hirta, Dryas octopetala, Primula scotica, P. stricta, Oxytropis lapponica, Papaver radicatum, Rhododendron lapponicum, Salix polaris, Veronica saxatilis,* etc.

If the soil, on the contrary, is deep and damp, as in morasses and along streams, or where water trickles down the sides of mountains, there is quite a different and more abundant vegetation, consisting of mosses with thickets of *Salix glauca, S. lanata, S. lapponum,* and *S. Myrsinites,* often with an undergrowth of *Aira alpina, Andromeda hypnoides, Cardamine bellidifolia, Cerastium trigynum, Eriophorum capitatum, E. vaginatum, Juncus biglumis, J. castaneus, J. triglumis, Koenigia islandica, Oxyria digyna, Petasites frigida,*

Ranunculus glacialis, R. nivalis, R. pygmaeus, Saxifraga aizoides, S. caespitosa, S. rivularis, S. stellaris, Silene acaulis, Tofieldia borealis, Vahlodea purpurea, Veronica alpina, etc.

V. THE LICHEN ZONE

This embraces the often stony tracts above the preceding zone, i.e., the highest mountain tops and the ground from which they rise.

Rocks and stones are here covered with the blackish yellow *Lecidea geographica* and other lichens. Where there is a little soil, some hardy mosses grow, and under favorable conditions a very few species of higher plants.

I may mention, as an illustration, that in 1877, when visiting the mountain Haarteigen (5,546 feet) in Hardanger, i.e., in the south of Norway, I noted the following higher plants upon the comparatively flat top of the mountain: *Carex rigida, Luzula arcuata, L. spicata, Lycopodium Selago, Poa alpina, Polygonum viviparum, Ranunculus glacialis,* and *Rhodiola rosea.*

As already repeatedly stated, all plant species are not strictly confined to the zone under which they are mentioned as especially characteristic factors. It is very general for species somewhat to overstep the boundaries of their true zone, either upward or downward. Certain species are even found in all zones from the sea to the snow, since they have a remarkable ability of adapting themselves to all kinds of soil and to all kinds of climatic conditions. As instances of such species we may mention *Calluna vulgaris, Empetrum nigrum, Eriophorum vaginatum, Festuca ovina, Nardus stricta, Polygonum viviparum,* and the species of *Vaccinium.*

Another circumstance is that typical mountain plants are sometimes found in the lowlands right down to the sea, e.g., in Jaederen, *Alchemilla alpina, Arctostaphylos alpina, Bartschia alpina, Saxifraga aizoides,* and *Selaginella spinulosa. Betula nana* occurs in the southeast of Norway down to fifty feet above the sea, and *Dryas octopetala* occurs at Langesund and at Varaldsö in Hardanger at sea-level. These occurrences were formerly often explained as relics of a previ-

ous age with a colder climate, but I do not think we need have recourse to such an explanation. In all the steep-sided valleys, typical mountain plants spread downward along streams and rivers, and often appear far below their real habitat. Whether they will remain there depends only upon their ability to compete with lowland plants and to withstand the night frosts in the spring after the snow has melted.

I assume, therefore, that the occurrence of the above-mentioned mountain plants in the lowlands is due to a chance carrying of seed to places that were favorable to the welfare of the species, e.g., limestone at Langesund and Varaldsö for *Dryas octopetala,* a peat-bog for *Betula nana,* and so forth.

THE IMMIGRATION OF THE NORWEGIAN FLORA

Geologists have long been agreed that Scandinavia and great parts of adjacent lands have once been covered with one entire ice-cap, as the interior of Greenland is at the present time. By degrees the view obtained that there have really been two such glacial epochs, separated by an intermediate warm period, in which the conditions probably more or less resembled those of the present day.

During the first, called the Great Glacial Epoch, the ice-cap extended as far as central Germany, over almost the whole of England, over the whole of Finland, and over a great part of northern Russia. It follows that under such conditions, all, or almost all, vegetation must have disappeared from the Scandinavian peninsula, from Norway and Sweden. I am inclined to believe that in places in Norway, the tops of high mountains rose above the ice-covering, and that a very few species of plants may have survived there; but this is a matter of no interest in the question upon which I shall now endeavor to throw light, namely, the immigration of the flora of Norway after the Last Glacial Period.

This was of considerably smaller extent. On the south the ice reached only as far as Mecklenburg, and the ice-boundary then ran obliquely northward up through Jutland in Denmark, of which, therefore, only a part was entirely covered with ice. There can be no doubt that the whole of

Sweden was covered by this ice-cap, but as regards Norway, the conditions are still a matter of dispute. Some geologists maintain that the ice went right out into the sea on all sides; others assume that in some parts there was an iceless coast-region, where only here and there great glaciers ran out into the sea.

The great majority of the species in the Norwegian flora must, however, have immigrated after the last Glacial Period; but with regard to their immigration and the conditions under which it took place, various theories have been advanced.

The first to take up this question, especially with regard to Sweden, was F. W. Areschoug ('66), who, in 1866, maintained that the present vegetation of Scandinavia was made up of at least three elements of different period and origin, namely:

(1) An arctic vegetation, which immigrated from the east during the latter part of the Glacial Period, and, from its origin, may be called the *North Siberian Flora;*

(2) A northeastern and eastern vegetation, which came into Europe from Siberia after the Glacial Period, but before the immigration of the beech. From its origin, it may be called the *Altai Flora;*

(3) A southeastern and southern vegetation, which came simultaneously with the beech, partly from the Caucasus and the countries 'round the Caspian and Black Seas, partly from the countries of the Mediterranean. This may be called the *Caucasian and Mediterranean Flora.*

Areschoug also pointed out that a number of arctic species in the north German and south Swedish lowlands must be regarded as relics of the vegetation of the high north, which, after the melting of the ice-cap, withdrew toward the north or up into the mountains.

This view received strong support in the discovery by A. G. Nathorst ('71) in 1870, in the fresh-water clays of the south of Sweden, of remains of typical arctic plants which do not grow there now, but only very much farther north, namely, *Betula nana, Dryas octopetala, Salix herbacea, S. polaris,* and *S. reticulata.*

In 1875, Axel Blytt ('76) first brought forward his well-known theory on the immigration of the flora of Norway during alternate wet and dry periods. According to Blytt's theory, the wild plants of Norway should be arranged in the following six groups: (1) the *arctic* (the mountain flora); (2) the *subarctic* (the vegetation of mountain and wooded slopes), which is more frequent in the arctic than in the more southern, lower regions; (3) the *boreal* (the vegetation of the rocky slopes covered with foliage trees), which has its widest distribution in the low land, but not the coast districts; (4) the *Atlantic* (Bergen coast vegetation), with distribution in the coast district, especially between Stavanger and Kristianssund; (5) the *sub-boreal,* which occurs in the southeast of the country, especially 'round the Kristiania Fjord; and (6) the *sub-Atlantic* (Kristianssand coast vegetation), which has its widest distribution in the coast district between Kragerö and Stavanger.

The arctic, boreal, and sub-boreal species of plants are warmth-loving, continental plants, while the subarctic, Atlantic, and sub-Atlantic keep chiefly to the coast districts and are insular in character. The former have immigrated during dry periods, the latter during damp periods, in the order in which they have been placed. Blytt assumed that within the period of history it is scarcely probable that any very great changes have taken place in climate or vegetation, and that the present is a dry period.

Blytt ('83) subsequently maintained that these changes of climate were due to cosmic causes, namely alterations in the eccentricity of the earth's orbit and alternate changes in the earth's position with regard to the sun, occupying periods of about 21,000 years. By the aid of this hypothesis he calculated the period from the conclusion of the Glacial Epoch down to the present time to be between 80,000 and 90,000 years. The damp and dry periods were thus of equal duration, namely 10,500 years.

As Blytt moreover started with the assumption that the plants could advance only step by step in their migrations, and could not be transferred direct from Denmark or England

to Norway, he supposed that the six different flora-elements had immigrated from the south through Sweden to the places in which they are now found, but during the subsequent change of climate had died out in the intermediate regions, in which they do not grow now.

Since then, Gunnar Andersson ('96, '06) has discussed this question with special reference to Sweden. He builds more particularly upon paleontological studies of the plants preserved in peat-bogs. He assumes that the climate, after the melting of the ice, continued to grow warmer until—since *Corylus Avellana,* according to fossil occurrences, had a far more northerly distribution area than at the present time—it showed a mean temperature in August that was about 2.5° C. higher than at the present time. The temperature has, therefore, fallen to that of the present day.

Gunnar Andersson designates the various periods after the Glacial Epoch according to the most characteristic plant, and assumes that the immigration has taken place in the following order:

(1) The *Dryas Flora* includes certain arctic species, e.g., *Dryas octopetala, Salix herbacea, S. polaris, S. reticulata, Oxyria digyna, Arctostaphylos alpina,* and others, which are supposed to have migrated into Sweden when the melting of the ice had begun, and followed this northward. The most northerly place, however, where these arctic plants are found in Sweden is in West Gothland, in about the latitude of Gothenburg. They have not been found, from this period, farther north.

(2) The *Betula odorata Flora* is more subalpine. With it came also *Salix aurita, S. caprea,* and *S. cinerea,* etc.

(3) The *Pinus sylvestris Flora* immigrated during a somewhat warmer period, which continued to grow warmer. In the lower, and thus older, part of the Pine Zone are found *Prunus Padus, Rubus idaeus, Rhamnus Frangula, Sorbus Aucuparia,* and *Viburnum Opulus*; in the upper, and therefore more recent, part, which has had a warmer climate, we find *Alnus glutinosa, Cornus sanguinea, Crataegus monogyna,*

Corylus Avellana, Tilia europaea, Ulmus montana, etc. Here we come to the transition to the next flora.

(4) *Quercus Flora,* which immigrated during the warmest period after the Glacial Epoch, when the mean summer temperature was about 2.5°C. higher than at the present day. In addition to *Quercus pedunculata* and *Q. sessiliflora,* there immigrated during this period *Acer platanoides, Fraxinus excelsior, Hedera Helix, Viscum album,* and a great number of warmth-loving plants, which have since kept to the warm slates and limestones.

As the last immigrants during the steady decrease of the summer temperature, Gunnar Andersson gives

(5) The *Fagus Flora* and (6) the *Picea excelsa Flora.*

What is new in this theory is that there is assumed to have been only one period with higher temperature since the Glacial Epoch. This, too, is supported by the results at which W. C. Brögger ('00) has arrived in his investigations of the Quaternary fossil mollusc fauna in the south of Norway.

Since then, the question of the immigration of the flora into Sweden has been treated in a series of papers by R. Sernander ('10), who rather inclines to A. Blytt's theory, and in Norway by J. Holmboe ('03), who subscribes to that of Gunnar Andersson.

The geological basis, however, upon which all investigations of the immigration of the flora into the Scandinavian peninsula must be built, has of late years undergone considerable alteration. A number of recent discoveries of fossil plants also give new points of support. There is still, however, uncertainty concerning many points, so that the opinions of geologists and phytogeographers by no means coincide.

In the first place, by counting the layers in stratified clay deposits in Sweden, Gerhard de Geer ('08) has succeeded in proving that not more than about 12,000 years have elapsed since the ice-cap of the last Glacial Period extended as far as Skaane in the south of Sweden. The ice had taken about 4,000 years to withdraw thus far from its southernmost boundary in Germany, and it afterwards took as much as about 3,000 years to withdraw to a range of terminal moraines

in central Sweden, and in the south of Norway to the morainic ridges that extend from Fredrikshald to Moss, Horten, Arendal, etc., and are designated by the Norwegian word "Ra."

According to G. de Geer, these great terminal moraines must have been formed about 9,000 years ago when the inland ice stood still along that line for a period of about 350 years. It is a matter of indifference to us that other geologists believe that this "Ra" period occurred somewhat earlier.

What is of great importance in the immigration of the flora, however, is that the extreme southeast of Norway and the center of Sweden, at the time of the "Ra" formation, lay much lower than at the present time, and sank still lower some time after the ice withdrew. It is supposed that the sea near Kristiania, during the "Ra" period, was about 660 feet higher than it now is, and a little later rose to 720 feet above its present height, which is the highest limit of the late glacial sea. But this limit differs in different parts of the country; it falls toward the coast, especially toward the west coast of Norway. At Larvik, for instance, it is about 426 feet; at Arendal, 246 feet; at Kristianssand, about 130 feet; at Mandal, 82 feet; and at Farsund, only 28 feet. Farther north it increases again, so that at Kristianssund it is about 246 feet, and at Trondhjem, 650 feet, or almost as great as at Kristiania.

THE DRYAS PERIOD

I have previously ('05) endeavored to show by *Dryas* and *Salix polaris,* which A. G. Nathorst has found in a fossil state in the south of Sweden, that the arctic flora cannot have made its way thence into Norway; for during the "Ra" formation the masses of ice went right out into the sea, and when the ice had withdrawn far enough to leave open land within the "Ra" line, the climate had already altered to such an extent that the arctic flora was extinct in the south of Sweden.

The earliest plants of which J. Holmboe ('03) has found remains in the southeast of Norway, prove also to be sub-

alpine; but farther west fossil arctic plants have been found in a number of places.

D. Danielsen ('09, '12) has found, between Kristianssand and Mandal, fossil leaves of *Salix polaris* from 46 to 59 feet, *Dryas octopetala* from 46 to 52 feet, and *Betula nana* from 46 to 52 feet above the sea. The uppermost marine boundary here is from 137 to 141 feet above sea-level, but the leaves are supposed to have been carried out by currents and deposited at a depth of perhaps 65 feet. Something similar may have taken place with most of those subsequently mentioned, as they are sometimes found covered with more or less loose material.

C. F. Kolderup ('08) has found, near Bergen, *Dryas octopetala, Salix polaris,* and *S. reticulata,* from 115 to 130 feet above the sea, while the marine boundary lies at a height of about 190 feet above sea-level.

J. Rekstad ('05, '06, '07, '08) has found *Salix polaris* 130 feet above the sea in Söndfjord, 187 feet above the sea in Nordfjord (marine boundary 250 feet above sea-level), and in Nordmöre sometimes 82 feet, sometimes from 344 to 377 feet, above sea-level; and *Salix herbacea* in Nordfjord 220 feet above the sea (marine boundary 360 feet above the sea), in Söndmöre 85 feet.

K. O. Björlykke ('00) has found *Salix reticulata* near Kristiania 540 feet above the sea, and near Trondhjem 340 feet above sea-level.

P. A. Oeyen ('04, '07) has found *Dryas octopetala* and *Salix reticulata* near Trondhjem at a height of 557 feet above sea-level, and *Salix polaris* in Asker, near Kristiania, 600 feet above the sea (the marine boundary at the latter locality is 692 feet above sea-level).

Remains have also been found of species that may have a subalpine occurrence, such as *Betula nana, Juniperus nana,* and *Salix phylicifolia;* but as they are less conclusive, they are not included here.

The point of especial interest is that these fossil plants on the west coast are found with remains of the high arctic mollusc *Yoldia arctica,* which is not now found on the shores

of Norway, but on the coast of Spitzbergen, and indicates a mean temperature of from —3 to —7°C. and thus quite an arctic climate. At Kristianssand these arctic plant-remains are found together with remains both of *Yoldia arctica* and *Mytilus edulis,* while *Salix polaris,* near Kristiania, is found with *Mytilus* and far below the highest marine boundary.

Two questions now present themselves, (1) did *Salix polaris* and other arctic vegetation continue to live during the Last Glacial Period upon a stretch of coast in the west and north of Norway that was not covered with ice, or (2) did *Salix polaris* and the other arctic plants immigrate from Jutland —where they lived during the Last Glacial Period—to the first land from which the ice disappeared at Kristianssand, and thence spread along the edge of the ice on both sides as the latter disappeared?

I have previously endeavored to uphold the first of these views as the more probable, having found ('05, p. 337) that the discoveries hitherto made of the remains of arctic plants favored the belief that 'during the Last Glacial Period there lived in Norway a high-arctic vegetation upon a strip of coast that was free from ice and must have extended about as far down as the Sogne Fjord. Subsequently, as time went on, several species of high-arctic plants that had immigrated from Russia and Siberia made their way for a greater or smaller distance southward in the north of Scandinavia.'

Various later discoveries of arctic plants all the way down to the south point of Norway go to prove that the iceless margin of coast may have extended thus far, at any rate partially. The isolated occurrence of *Saxifraga Aizoon,* growing upon the mountains in inner Ryfylke, east of Stavanger, is also difficult to understand unless it is assumed that it migrated thither from an iceless margin of coast, as this species, beyond being found in the Alps, is only known in Nordland in Norway, and in Iceland and Greenland.

But it seems probable that here a number of vegetable species from the interglacial period may have survived the Last Glacial Period. This must have been the case with

Artemisia norvegica, whose province of distribution in Norway is on the Dovre and adjoining mountains in the northwest (Troldheimen), some of which could scarcely have been covered with ice during the Last Glacial Period. It is even possible to name, with considerable accuracy, some of these plants, as they form the "Greenland element" in the arctic flora of Norway. I designate as such those plants which Norway has in common with Iceland, Greenland, or the north of North America, but that are not found in western Siberia. These are as follows:

Arnica alpina is found in the north of Norway from Salten to Alten, and also in the north of Sweden, on the Kola Peninsula and Novaja Semlja, but not again until the east of Siberia is reached. It is also found in Greenland and on the Alps.

Campanula uniflora is found in Norway from Lom to Reisen, in Swedish Lapland and Novaja Semlja, but elsewhere only in Greenland and arctic North America.

Carex nardina is found in Norway from Salten to Kvaenangen, and in Swedish Lapland, but elsewhere only in Iceland, Greenland, and arctic North America.

Carex scirpoidea is known in Norway in Salten, and elsewhere only in eastern Siberia and western Greenland.

Draba crassifolia is found in Norway, 'round Tromsö, but otherwise only in Greenland.

Pedicularis flammea is found in Norway from Salten to Lyngen, and in Swedish Lapland, but elsewhere only in Iceland and Greenland.

Platanthera obtusata is found in Norway in Reisen and Alten, but otherwise is known only from eastern Siberia and arctic North America.

A fact that possesses peculiar interest in the study of the occurrence of these and other similar species of plants in the Norwegian mountains, is the discovery in central Norway of interglacial remains of *Elephas primigenius* and *Ovibos moschata.* These great mammals became extinct at the beginning of the Last Glacial Period, but some of the plants that lived at the same time found a dwelling place upon the iceless

coast margin and there managed to survive that period, and then to some extent followed the retreating ice up to the mountains where they are now found.

Andr. M. Hansen ('04, '04[a]) even assumes that at least 300, perhaps as many as 500, kinds of vascular plants may have lived upon this supposed iceless strip of coast, which he assumes to have been fairly broad. These figures are perhaps rather high, but it is not possible to make more exact statements until paleobotanical investigations have been carried out in the peat-bogs in these regions.

Against the second possibility, namely, that the arctic plants may not have immigrated from Denmark to Kristianssand until after the ice had withdrawn, several facts may be cited.

These arctic plants, farther up the west coast of Norway (e.g., in Nordfjord), are found together with *Yoldia arctica,* and thus in a decidedly arctic climate, while those near Kristianssand, though, indeed, found with *Yoldia,* also occur with *Mytilus,* which indicates that the climate was somewhat milder and that the plants originated at a more recent period than those in Nordfjord. Thus the arctic plants, e.g., those in Nordfjord, cannot have immigrated thither from Kristianssand, but may be assumed to have been there during the Last Glacial Period.

On the other hand, *Salix polaris* near Kristiania, which appears to have originated at a somewhat later period, may have been able to immigrate thither along the margin of the ice from Kristianssand; but this cannot at present be stated with certainty, as no fossils have been found between the two points.

THE BETULA ODORATA PERIOD

As the ice-cap withdrew and the climate became milder, the land began to rise. In the center and south of Sweden, this took place so rapidly that a land connection was formed between Sweden and Denmark, and also between south and north Sweden, very much as it is at present. The Baltic thereby became a lake, its waters becoming gradually fresher and containing fresh-water animals, especially *Ancylus fluvia-*

tilis, which has given to this geological period the name of the Ancylus Period.

By this upheaval of the land, a broad migration road for

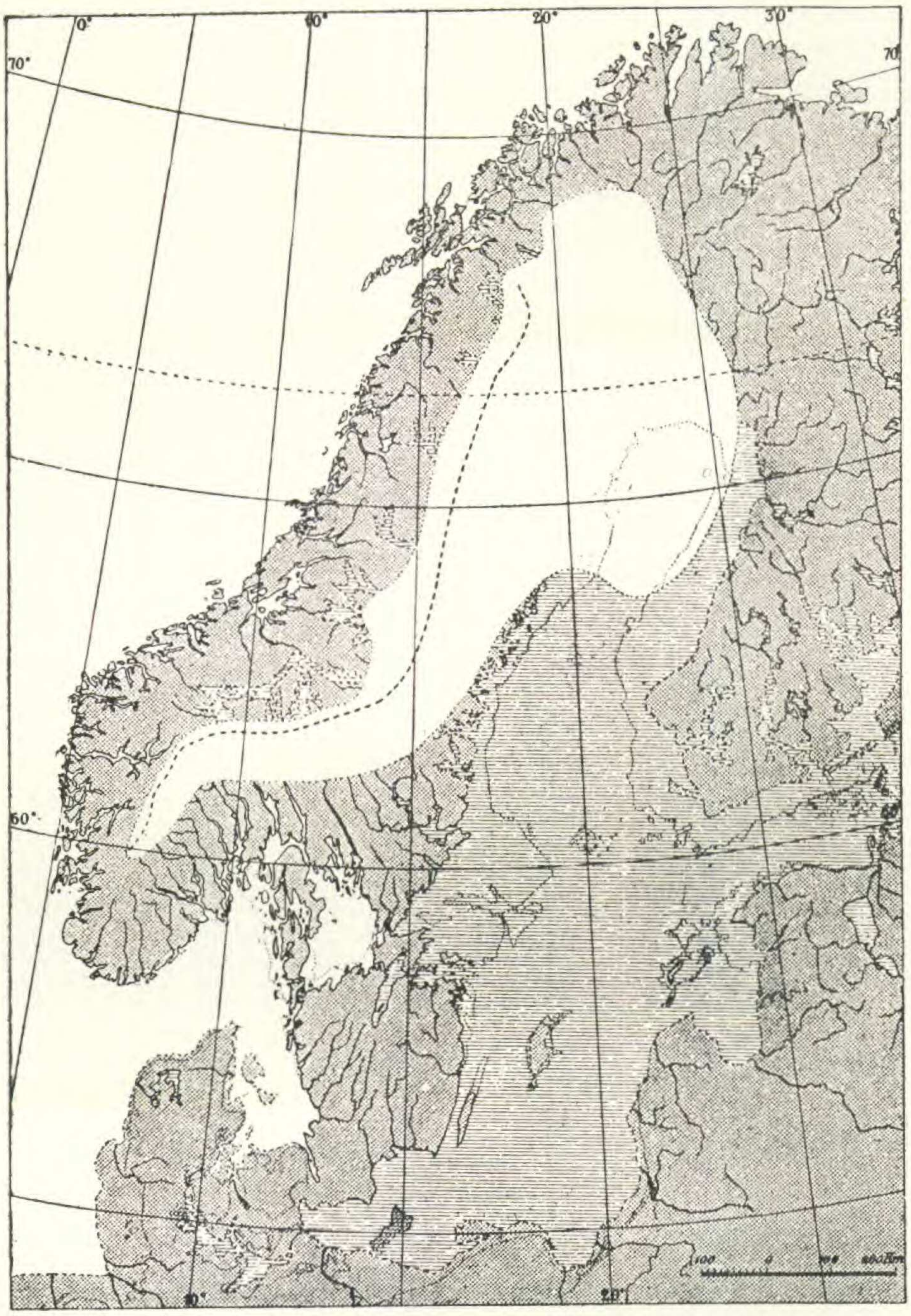

Fig. 4. Map of Scandinavia during the Ancylus Period: the white area represents the remainder of the great ice sheet; region indicated by parallel horizontal lines represents lake (water); region indicated by oblique cross-lines represents land.—Chiefly after De Geer.

plants was opened from the southeast and east to Norway. Seeds were probably carried over now and again before this upheaval of the land—as soon as land was vacated by the

ice in the southeast of Norway; but the direct land connection facilitated the spread of all species of plants.

Betula odorata was an early immigrant, and with it were a number of other plants of which fossil remains have been found, especially in peat-bogs in the southeast of Norway,[1] namely, *Betula nana, Carex ampullacea, C. filiformis, Cicuta virosa, Comarum palustre, Empetrum nigrum, Equisetum fluviatile, Hippuris vulgaris, Juniperus communis, Menyanthes trifoliata, Myriophyllum spicatum, Nymphaea alba, Potamogeton natans, Scirpus lacustris, Vaccinium Vitis-Idaea, Zannichellia polycarpa.*

But in addition to these, it may probably be assumed that the following species, which are found as subfossil remains from the subarctic or partially arctic period in Swedish peat-bogs,[2] may have migrated into Norway by this southeastern road as soon as some of the nearest land areas were free from ice. These are *Andromeda polifolia, Arctostaphylos alpina, A. Uva Ursi, Batrachium confervoides, Diapensia lapponica, Montia fontana, Myrtillus uliginosus, Oxyria digyna, Phragmites communis, Polygonum viviparum, Populus tremula, Potamogeton filiformis, P. praelongus, Salix aurita, S. caprea, S. cinerea, S. phyllicifolia, S. repens, Scheuchzeria palustris,* and *Stachys sylvatica.* During this period *Hippophaë rhamnoides* also immigrated to Sweden, but as it spread along the east coast of that country and thence through Jemtland to the north of Norway, this could not have taken place until much later, after the last of the central inland ice had melted.

THE PINUS SYLVESTRIS PERIOD

After *Betula odorata,* but during the so-called Ancylus Period in Sweden, *Pinus sylvestris* migrated to the southeast of Norway, while the climate was still comparatively cold; but, as we may gather from some of the plants that occur, especially in the latter part of the pine zone, the temperature became rather rapidly warmer.

J. Holmboe has found in the peat-bogs of Norway the following fossil plants in the pine zone: *Alisma Plantago, Alnus*

[1] By J. Holmboe ('03).
[2] By Gunnar Andersson ('96).

glutinosa, A. incana, Andromeda polifolia, Betula verrucosa, Carex Pseudocyperus, Cladium Mariscus, Corylus Avellana, Eriophorum vaginatum, Isoetes lacustris, Linnaea borealis, Lycopus europaeus, Naias marina, Nuphar luteum, Oxycoccus microcarpus, Rhamnus Frangula, Rubus Idaeus, Salix aurita, Scheuchzeria palustris, Solanum Dulcamara, Spiraea Ulmaria, and *Ulmus montana.*

In addition to these, Gunnar Andersson has found in Swedish peat-bogs from the pine period the following species: *Calla palustris, Caltha palustris, Carex riparia (?), C. vesicaria, Ceratophyllum demersum, Cornus sanguinea, Crataegus monogyna, Eriophorum angustifolium, Galium palustre, Iris Pseudacorus, Myriophyllum alterniflorum, Naias flexilis, Myrtillus nigra, Naumburgia thyrsiflora (?), Oxalis Acetosella, Pedicularis palustris, Potamogeton pectinatus, Prunus Padus, Ranunculus repens, Rubus saxatilis, Rumex Hydrolapathum, R. maritimus, Sorbus Aucuparia, Sparganium ramosum, Thalictrum flavum, Tilia cordata, Viburnum Opulus,* and *Viola palustris.*

But several of these latter species did not get as far as Norway until the succeeding warmer period, and we shall therefore find them again in the list of fossils that have been found in peat-bogs from the Oak Period. A few of them may also have immigrated by other routes, as a land connection with Sweden was established not only in the south but also in the east, the ice having withdrawn to the interior of the country, and at the close of the Ancylus Period probably melted away entirely. Various discoveries go to prove, for instance, that *Alnus glutinosa* migrated into Norway from the south, while *Alnus incana* came from the east.

There are in Norway two quite distinct forms of *Pinus sylvestris* L., which by some botanists are given as species, namely, var. *septentrionalis* Schotte, and var. *lapponica* (Fr.) Hn. The second of these, which is found in abundance in Finland and the far north of Sweden, also grows in Norway, especially in the north, and on the mountains farther south, where here and there it pushes down into the valleys. It may be assumed that this *P. sylvestris* var. *lapponica* did not im-

migrate from the northeast until much later—after the ice-cap had melted in the north of Norway and Sweden, and then made its way southward. The common *Pinus sylvestris,* on the contrary, as we have said, undoubtedly migrated into Norway from the southeast through Sweden, which is probably the way by which most of those species immigrated which are now found growing with it in the southeast of Norway.

THE QUERCUS PEDUNCULATA PERIOD

The climate gradually becomes warmer, the inland ice has quite disappeared, and simultaneously with its disappearance the land in a belt across central Sweden begins once more to sink (the Littorina Subsidence). When this subsidence culminated, the south of Sweden was a great island which, on the south, was separated—as it now is—from Denmark by Oeresund and by a broad arm of the sea, which ran from Skagerak through the district in which the lakes Venern and Vettern now lie right to the Baltic. This sea thus acquired an opening into the North Sea, and its waters gradually became salt.

This subsidence of the land, which took place when the land around Kristiania was about 230 feet lower than it now is, did not greatly affect Norway, for it amounted in the latter to only a few yards. But it may probably be assumed that so great an arm of the sea, with a current of Gulf Stream water that even brought Gulf Stream nuts (*Entada gigalobium*) with it to the shores of Bohuslaen—whence they are not carried at the present day—must have made the climate warmer and more insular than it now is. Before the subsidence, then, the climate must have been warm and dry, after the subsidence, warm and damp.

How much warmer the climate must have been is apparent from Gunnar Andersson's investigations—following the discovery of fossils—on the distribution of *Corylus Avellana* at that time, compared with its present distribution. It appears that the mean temperature of the summer months must have been about 2.5°C. higher than it now is. In the sea off the coast of Norway there lived at that time species of the more

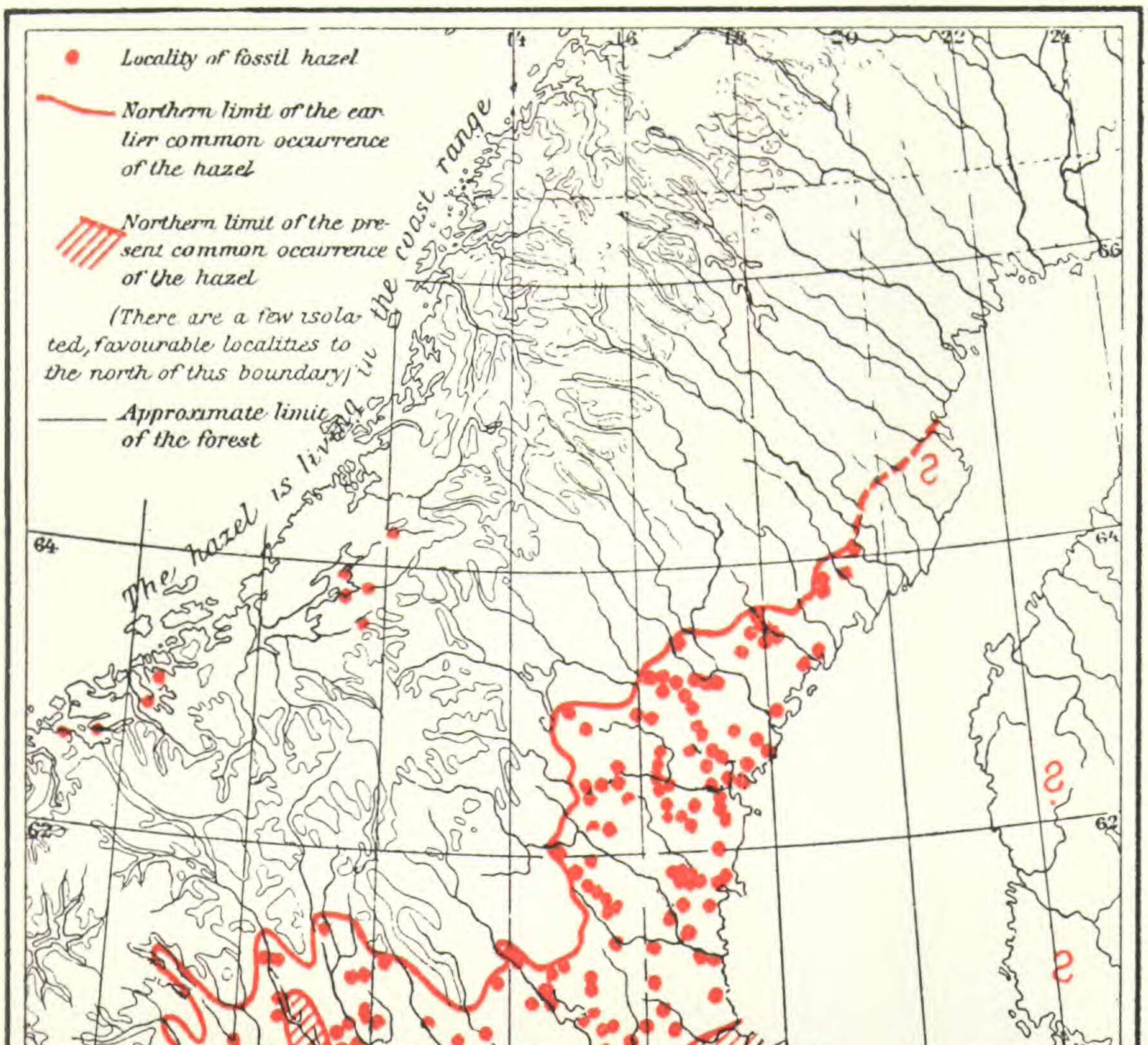

Fig. 5. Map of the present and the former distribution of *Corylus Avellana* in Sweden. The entire area from which *Corylus* has disappeared is about 32,420 square miles. (For key, see upper left-hand corner of figure.)—After Gunnar Andersson.

southern mollusc genus *Tapes*, which shows that the average annual temperature must have been between 8 and 9°C. (Brögger, '00).

Various opinions have been expressed as to whether the warmest period was before, at, or a little after, the maximum of the Littorina Subsidence in Sweden. This is of little importance here, but what is more important is that the earliest remains of stone implements in Norway date from this warmest period (the Tapes Period), which, therefore, in the opinion of archaeologists, must be assumed to have been about 7,000 years ago. This accords well with G. de Geer's calculations from the number of clay strata.

J. Holmboe has found the following species of plants, together with *Quercus pedunculata,* in Norwegian peat-bogs: *Acer platanoides, Aspidium Thelypteris, Bidens cernua, B. tripartita, Calla palustris, Carex stellulata, C. vesicaria, Ceratophyllum demersum, Crambe maritima, Fraxinus excelsior, Galeopsis Tetrahit, Iris Pseudacorus, Myrica Gale, Naias flexilis, Naumburgia thyrsiflora, Oxalis Acetosella, Peucedanum palustre, Potamogeton praelongus, Ranunculus repens, Rubus fruticosus, Ruppia rostellata, R. spiralis, Scirpus maritimus, Sorbus Aucuparia, Sparganium ramosum, Stachys sylvatica, Thalictrum flavum, Tilia cordata, Viola sp., Zostera marina.*

It will at once be seen that a good many of these species were enumerated as having been found in the south of Sweden during an earlier period, i.e., with *Pinus sylvestris.* This agrees very well with the assumed immigration route through Sweden, as it must have taken a considerable length of time for these plants to spread through Sweden into southern Norway. It must not, however, be forgotten that the occurrences of plants in the peat-bogs indicate only the minimum length of time of their existence in the place in question, as they may very well have lived there for a long time before being deposited in a peat-bog, to be found there through the investigations of a botanist.

In addition to the above, Gunnar Andersson has found the following fossil species in the Oak Period in Sweden, these

species being either unknown in Norway or found only in later deposits, some of them probably not having immigrated until later, together with *Picea excelsa.* They are *Angelica sylvestris, Cakile maritima, Cornus suecica (?), Helianthus peploides, Hedera Helix, Ledum palustre (?), Potamogeton crispus, Ranunculus Flammula, R. sceleratus, Sagittaria sagittifolia,* and *Viscum album.*

A. Blytt ('82) assumed that a great many warmth-loving species, constituting what he called the "boreal flora," must have immigrated at this time, especially several xerophilous plants, such as a number of *Labiatae, Boragineae,* etc. (some of which are now commonly found on the steppes of southern Russia), which still keep especially to warm slates and limestones in the Norwegian lowland in the east, the west, and the province of Trondhjem.

Andr. M. Hansen ('04) draws especial attention to the following among these species, constituting what he calls the "Origanum community," and which grow on open slopes with a very sunny exposure: *Agrimonia Eupatoria, Androsace septentrionalis, Arenaria serpyllifolia, Calamintha Acinos, Campanula Cervicaria, Carex muricata, Centaurea Scabiosa, Dianthus deltoides, Echinospermum lappula, Origanum vulgare, Plantago media, Polygala amara, Ranunculus Polyanthemos, Torilis Anthriscus, Trifolium medium, Turritis glabra, Verbascum nigrum,* and *V. Thapsus.* As they grow upon dry slopes, it is not very probable that remains of them will be preserved in peat-bogs or elsewhere. Paleontologically, therefore, their immigration cannot be determined, but something may be concluded as to their occurrence in the present day; for it appears that this warmth-loving plant community has its most connected province of distribution from the lowlands of the southeast of Norway, on the warm slates through Valdres and Gudbrandsdal, and are then met with once more on the low land of the western fjord valleys, and in the province of Trondhjem. To this last locality there is evidently also an immigration road through Jemteland from the east coast of Sweden. On the other hand, this plant community is wanting throughout so great a part of the

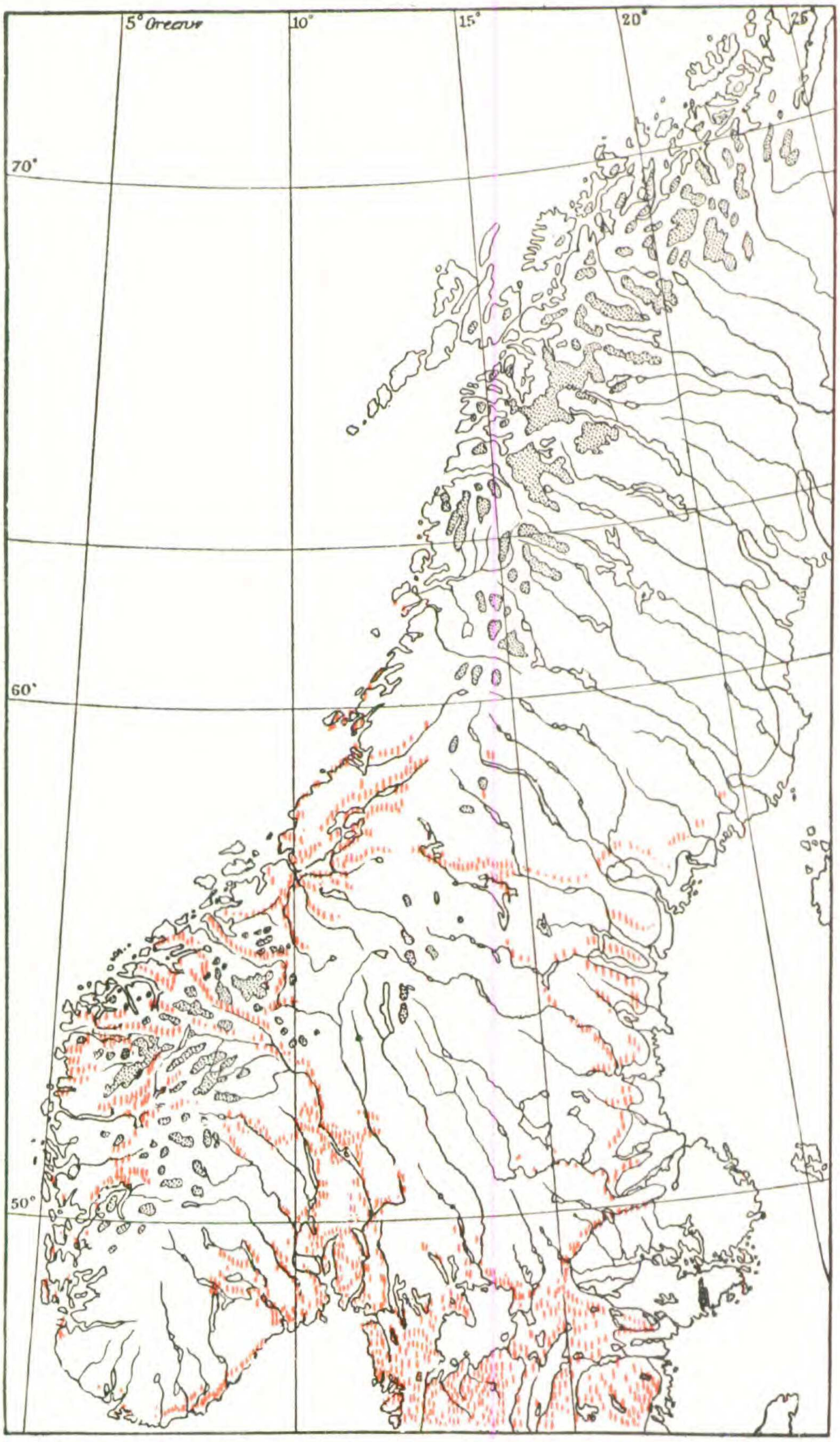

Fig. 6. Sketch-map showing the distribution and journeys of the *Origanum* community (vertical red lines) in Scandinavia. The extent of the montane region during the warmest post-glacial period is indicated by black-dotted areas.—After Andr. M. Hansen.

southwestern lowlands, that it can hardly be imagined that it migrated along the coast to the west and Trondhjem.

It must therefore be taken for granted that these plants migrated by way of the mountain passes, some of which now lie at such an altitude that even *Pinus sylvestris* cannot live in the highest localities. But I have already mentioned that the summer temperature during this period was about 2.5°C. higher than it now is. We see, moreover, that remains of pine forests are found on the mountains in Norway, e.g., on the Dovre Mountains in central Norway, and on the Hardanger plateau in the south of Norway, respectively 990 and 1,470 feet above the present highest limit of *Pinus sylvestris.* Under the then existing climatic conditions, the now treeless passes were clothed with forest, and warmth-loving plants were able to spread through them.

A. Blytt, and after him R. Sernander, distinguishes between a boreal and a sub-boreal flora, the members of which are supposed to have been lovers of warmth and dryness, but separated in their immigration by an Atlantic flora that loved humidity and warmth. With this I cannot agree. Several of the species that Blytt ('82) classes under "sub-boreal" are found in a fossilized state together with those he calls "boreal"; and around Kristiania many species of these so-called different floras grow together under exactly the same conditions in the same localities.

It seems likely, however, that the climate was more humid during the Littorina Subsidence, when the water of the Gulf Stream could make its way directly into the Baltic across central Sweden. A. Blytt ('82, p. 23) says: "Man darf deshalb mit einem hohen Grad von Wahrscheinlichkeit behaupten, dass die atlantische Flora in dieser Regenzeit eingewandert ist, und ihren Weg rund um den Christianiafjord gefunden hat (in derselben Weise, wie unter der folgenden Regenzeit die subatlantische)." I cannot agree in all respects with this. Those forms which Blytt calls "atlantische Arten" include a great number of species, of which some occur in what I have here called the "region of Ilex Aquifolium," others constitute what I have called the "west European

coast flora," while among other species belonging to Blytt's group *Rhynchospora alba, Alnus glutinosa, Myrica Gale, Arnica montana, Erica Tetralix, Ranunculus Flammula, Lychnis Flos-cuculi,* etc., may be mentioned, which grow on the low-lying land in many parts of southern Norway. As a rule, they prefer, it is true, damp places, but some species go right up to the Birch Zone on the mountains, so they may be presumed to have immigrated from the southeast through Sweden; but there is nothing to prove that this took place just at the maximum of the Littorina Subsidence. As instances, indeed, of the contrary, *Alnus glutinosa* from the Birch Period and *Myrica Gale* from the Oak Period are found in Norwegian peat-bogs and were, therefore, much earlier.

I believe that the west European coast flora on the west coast of Norway immigrated directly, by fits and starts, from England; but we will return to this later on.

THE PICEA EXCELSA PERIOD

According to archaeological calculations, the Scandinavian Stone Age lasted about 3,000 years, so that the Bronze Age in Scandinavia began about 4,000 years ago. During this period the climate was undoubtedly warmer than it now is, and it was not until the Bronze Age that any noticeable fall seems to have taken place.

At the beginning of the Stone Age the land around Kristiania lay 230 feet lower than at present, but during the Stone Age it was elevated about 184 feet, and during the Bronze Age it rose to about its present height above sea-level.

In the Bronze Age, or perhaps in the latter part of the Stone Age, *Picea excelsa* migrated into Norway from the east, from Finland through Sweden. In Finland it is still found as a fossil in the Oak Period, and in Sweden, especially in the north and east, it is so found, while spruce is not found fossilized in the south of Sweden or Denmark after the Glacial Epoch.

In the north of Norway (Finmark) there are occurrences of spruce that are entirely independent of the spruce's great province of distribution in the south of Norway. It appears

that these northern occurrences are of a distinct form (*Picea excelsa* [Lam.] Link f. *obovata* Ledeb.), which is classed by some botanists as a separate species, and has its distribution through the north of Finland and Russia. There can, of course, be no doubt that the spruces in these northernmost occurrences immigrated independently from Finland, and probably at a later period, as there is a tradition that they were imported thither by human beings (Lapps).

According to J. Holmboe, *Calluna vulgaris* came into Norway during the same recent period in which *Picea excelsa* made its appearance, but there is no doubt that the former immigrated from the west and then spread eastward, i.e., in the direction opposite to that in which *Picea excelsa* spread. Both these species have now a very wide distribution in Norway.

Strange to say, there has not been found in the deposits from the Pine Period in Norwegian peat-bogs a single plant that is not to be found in the earlier periods. In Sweden the only new species found is *Rubus Chamaemorus,* which, however, undoubtedly grew there long before, as it must on the whole be considered to be a subalpine species. This is sufficient to show that special conditions are necessary in order that parts of plants may be preserved in bogs, and that it will, therefore, always be only a small proportion of the plants growing around the bogs which will be so preserved.

It is strange, for instance, that *Taxus baccata* is not found in Norwegian peat-bogs. It is found as a fossil from the Oak Period in Sweden, and must have been far more common in Norway in the early Iron Age than it is at the present time, as H. Conwents found, on examining twenty-three vessels in the Archaeological Museum in Kristiania, that eighteen of them were of *Taxus* and only one of *Picea excelsa.*

According to R. Sernander ('10) the period of greatest warmth must have occurred in the Bronze Age, and he believes that it was then that *Corylus Avellana* was most widely distributed northward. The Bronze Age, however, judging from the molluscs that were then found off the south coast of Norway, seems to have had a cooler climate than that of the

Tapes Period, i.e., the Scandinavian Paleolithic Age. On the other hand, R. Sernander believes that at the beginning of the Iron Age—about 2,400 years before our own day—so great a decline in temperature ensued that the montane plants made their way into the lowlands in many places. He interprets the present occurrences of alpine plants in the lowlands as relics from that period. This can, however, be the case only to a certain extent, for there is no doubt that at the present day alpine plants spread down to the lowlands and continue to grow there, provided the conditions are favorable. R. Sernander gives to his assumed cold, damp period at the beginning of the Iron Age the name employed by A. Blytt, the "sub-Atlantic period"; but the two have, in reality, very little to do with one another. A. Blytt states that his sub-Atlantic period occurred when the south coast of Norway lay from 30 to 50 feet lower than its present level, which would answer to the beginning of the Bronze Age. He mentions, among other species that immigrated during the sub-Atlantic period, *Carex Pseudocyperus* and *Cladium Mariscus,* which had already immigrated in the Pine Period, and *Ceratophyllum demersum,* which had immigrated in the Oak Period, besides two or three species that were certainly imported later in foreign grain and grass seed.

I do not yet consider R. Sernander's cold, damp "sub-Atlantic period" at the beginning of the Iron Age to have been clearly proved, although there are a few facts that speak in its favor. But even if such a cold, damp period did supervene, its principal effect would have been to decimate the oak flora—in localities that were not especially warm—more rapidly than if the climate had gradually become colder from the Stone Age to the present time, as most people believe. Similarly, it may have promoted the occasional descent of montane plants to the lowlands, but it appears that this can also take place under the present climatic conditions, without the necessity of having recourse to relic occurrences from the "sub-Atlantic" or even from the "Dryas Period."

An instance of such an occurrence is that of *Dryas octopetala* at Langesund in southeastern Norway. This species

is found there right down to the level of the sea, and is very common on the limestone of the locality. Together with J. Holmboe ('03), I have endeavored to prove that over the whole of the area in which *Dryas* appears, the latter can scarcely have existed for more than 100 years. I cannot ascribe any convincing power to the objections that have been raised against this line of argument.

THE FAGUS SYLVATICA PERIOD

In Norway, as already mentioned, *Fagus sylvatica* grows upon the southeast coast, with Larvik as a center. There is, in addition, an isolated beech-wood in Seim, to the north of Bergen, 280 miles from the nearest occurrence of beech.

It was formerly believed by A. Blytt that this beech-wood in Seim was a relic of a connected distribution of beech along the coast; but no discovery of fossils favors this idea. On the contrary, these two occurrences of beech appear to be perfectly independent of one another.

J. Holmboe ('05, '09) has endeavored to find out when the beech appeared at Larvik and in Seim. He has come to the conclusion, judging from what has been found in the peat-bogs, that at Larvik the beech immigrated considerably later than *Picea excelsa.* It can thus actually be assumed to have immigrated in the Iron Age, or perhaps as late as the time of the Vikings. This late immigration is in harmony with the fact that in the southeast of Norway the beech is making very rapid advance at the present time. Holmboe says that the beech-wood in Seim, from a geological point of view, is very recent, but that in any case its age should scarcely be put lower than about 1,000 years.

It seems to me most probable that the beech was introduced into Norway by man in the time of the Vikings, when there was ample communication with those countries in which this so generally useful tree formed extensive forests. In Seim, near Bergen, where the beech grows, the Norwegian King Haakon the Good, who was educated in England at the court of King Athelstan, and reigned from 935 to 961, had one of his estates; and it is not unnatural to suppose that he may

have tried to introduce a tree that he knew so well from his childhood and youth in England.

It is certain that in the course of time man has assisted in introducing many species of plants, some consciously, as, for instance, plants for cultivation, others by chance and unconsciously.

In the famous Viking ship from Oseberg, which is believed with certainty to have originated in the first half of the ninth century, fruit, seeds, and other remains of plants have been found, and have been determined by J. Holmboe ('06). The following cultivated plants were among them: *Avena sativa, Corylus Avellana, Isatis tinctoria, Juglans regia, Lepidium sativum, Linum usitatissimum, Pirus Malus,* and *Triticum vulgare.* As *Isatis tinctoria* is found growing apparently wild, in certain places in Norway, there can scarcely be any doubt that it has found its way thither from localities where it had previously been cultivated as a dye-plant. This is probably also the case with *Serratula tinctoria* in Jaederen, near Stavanger. The weeds found in the Oseberg ship were as follows: *Capsella Bursa-pastoris, Chenopodium album, Galeopsis Tetrahit, Lamium (purpureum?), Polygonum Convolvulus, Stellaria media,* and *Urtica urens.* Several of these, it is true, had immigrated earlier, as has been said of *Galeopsis Tetrahit;* but it shows that as early as the time of the Vikings, there were opportunities of importing foreign weeds.

In monastery gardens various medicinal, household, and ornamental plants were cultivated, and one is inclined to believe that several of these which now have quite a wide distribution in Norway, e.g., *Aquilegia vulgaris, Berberis vulgaris, Sambucus nigra,* etc., originally spread with the monasteries as centers.

It is still easier to demonstrate a number of species of weeds that have been imported recently, and of which some appear to have a really astonishing power of spreading. J. Holmboe ('00) has traced the spread of the following weeds from the year when they were first observed in Norway: *Alyssum calycinum* (1857), *Anthemis tinctoria* (1772?, 1807), *Barbarea vulgaris* (1790), *Berteroa incana* (1826), *Bunias*

orientalis (1812), *Campanula patula* (1870), *Cerastium arvense* (1817), *Chrysanthemum segetum* (1704), *Cotula coronopifolia* (1875), *Conringia orientalis* (1859), *Erigeron canadensis* (1874), *Galinsoga parviflora* (1880), *Lepidium perfoliatum* (1875), *L. virginicum* (1889), *Matricaria discoidea* (1850), *Rudbeckia hirta* (1880), *Senecio viscosus* (1804-1808), *Thlaspi alpestre* (1874), and *Xanthium spinosum* (1872). Some of these plants are now among the most troublesome weeds in large and small areas in Norway.

There can, I suppose, be no doubt that man, directly and indirectly, in the 7,000 years in which he has lived in Norway and maintained a lively intercourse—especially during the last 2,000 years—with the rest of Europe, must have assisted in introducing a great number of plants in addition to the above named. Among the former may be mentioned *Agrostemma Githago, Anchusa arvensis, Anthemis arvensis, Avena fatua, Brassica campestris, B. nigra, Bromus secalinus, Carduus crispus, Centaurea cyanus, Chenopodium capitatum, C. hybridum, C. glaucum, C. polyspermum, C. rubrum, Circium arvense, Convolvulus arvensis, Euphorbia Helioscopia, E. Peplus, Fagopyrum tataricum, Fumaria officinalis, Galeopsis angustifolia, G. Ladanum, G. speciosa, Galium Aparine, G. Mollugo, Lolium temulentum, Matricaria Chamomilla, Raphanus Raphanistrum, Sinapis alba, S. arvensis, Sonchus asper, S. oleraceus, Spergula arvensis, Spergula vernalis, Thlaspi arvensis,* etc. In addition to these there are a great many species that are generally classed in the floras under the heading "run wild" or "perhaps originally run wild," and concerning which it may certainly be assumed that they have been introduced by man's mediation in some way or other.

It is no longer possible to maintain the old dogma which held that the entire plant community migrated step by step, like a regiment of soldiers, and took possession of the country under climatic conditions that were favorable to the various species, while the previous vegetation was decimated and only survived in especially favorable localities; for *vegetable*

species generally immigrate singly and independently of one another.

It is not only man that assists in carrying plants across large sea surfaces; the wind, ocean currents, and especially birds from time to time transport seeds and other parts of plants, which, under favorable conditions, continue to grow.

I will not here go further into this complex question in its entirety, but will refer to R. Sernander's ('01) detailed work on the conditions for spreading in a great number of Scandinavian plants. I must, however, mention a few examples of probable, or certain, chance distribution. At Vaage Lake, far up the valley Gudbrandsdal, 990 feet above sea-level and separated from the innermost fjords of the west coast by 56 miles of very high mountains, grows the typical sea-shore plant, *Elymus arenarius.* That this occurrence represents a relic is absolutely out of the question, for the sea cannot have reached the height of Vaage Lake since the Silurian Period. But I have seen gulls flying over the lake, and they may possibly have carried seeds with them, which have found a favorable soil in the long sandy shores.

In 1837, *Coleanthus subtilis* was found upon a flooded river bank a little north of Kristiania, and in 1842 a great number of specimens were collected in the same locality, probably all that existed there, for in spite of the most careful search for a number of years, the plant has never subsequently been found in that or in any other place in Norway. As its nearest habitat is in Bohemia, it can only be supposed that some wading bird, in rapid flight from Bohemia to Norway, brought the seed with it; and, furthermore, that as the seed fell upon favorable soil, the plant grew up and had already begun to spread when the collection was made in 1842.

I have already ('05) endeavored to show that *Campanula barbata,* which occurs in a limited area on the mountains of central Norway, and is not again found until we come to the mountains of Central Europe, cannot be a glacial relic, but must have been accidentally introduced into Norway (by birds?) in recent times.

Judging from the distribution in the present day of a number of plants on the south and west coasts of Norway, it seems natural to assume that they have been brought directly over the sea from the nearest country, Denmark or England. It was thus not necessary for them to move step by step by the long route through Sweden, or even round the Kristiania Fjord, to reach their present habitats. The latter is all the less probable from the fact that certain of them seem to have been imported quite recently, when the climatic conditions cannot have been very different from those which exist at the present time. The following are instances of these:

Aera setacea grows in Norway from Kristianssand to Stavanger. The species is common in Jutland in Denmark, but in Sweden is found only in the extreme south.

Airopsis praecox is found from Kragerö to Nordmöre. It occurs, it is true, in Sweden, from the south up to Vestergothland and Bohuslän; but from that region to Kragerö is considerably farther than from Jutland, where the plant is found in abundance.

Corydalis claviculata is found from Kristianssand to Haugesund. It grows wild in Denmark and England, but not in Sweden; I assume, therefore, that it immigrated from one of the former countries.

Galium saxatile is found from Kristianssand to Nordmöre. It grows in Sweden from Skaane to Bohuslän, but it is far more probable that it came from Jutland, where it is common.

Genista tinctoria is found only at Brevik, and must have been recently imported, as there are only a few specimens of it. It is found wild only in southern Sweden, but is common in Jutland.

Geranium columbinum is found in the district extending from Kragerö through the west of Norway to the Trondhjem Fjord. In Sweden it has an eastern distribution from Skaane to Upland. It is common in Denmark.

Heracleum australe is found from Kragerö to Söndfjord. It occurs in Sweden from the south right up to Vermeland, but the distance from this district to Kragerö is considerably greater than that from Jutland, where it also occurs.

Hydrocotyle vulgaris grows here and there from Larvik to Bergen. In Sweden it does not extend farther than to Dalsland, but it is exceedingly common in Jutland.[1]

Hypericum pulchrum grows in the region extending from Larvik through the west of Norway to the Trondhjem Fjord. In Sweden it is found from Halland to Bohuslän, but it is more natural to suppose that it immigrated from Denmark or England, where it is common.

Luzula sylvatica grows along the coast from Arendal to Lofoten. It is found wild only in the south of Sweden, but is common in Jutland.

Rubus Radula is found from Kragerö to Mandal. In Sweden it is found from Skaane to Bohuslän, but is very common in Jutland.

Sarothamnus scoparius grows between Grimstad and Mandal. In Sweden it is wild only in the east. It is very common in Denmark.

Scirpus multicaulis grows at Arendal and in Jaederen. It is found in Sweden from Skaane to Vestergothland. It is common in Denmark.

Scirpus setaceus is found to the west of the Kristiania Fjord and more recently has been found also along the coast almost as far as Bergen. It is found in Sweden from Skaane to Bohuslän, but it can scarcely be supposed to have migrated thence to its most easterly occurrence in Norway, as the center of its distribution in Sweden lies farther south, and in Norway farther west. It seems, therefore, more probable that it has been brought to Norway directly from Denmark.

[1] Since writing the above, I have discovered *Hydrocotyle vulgaris* in a locality on Kirkeöen (Hvaler) in southeastern Norway. The locality lies about midway between the easternmost of the previously known Norwegian stations and the Swedish localities and might be looked upon as proof that the species in question had immigrated step by step through Sweden and not directly from Denmark. This, however, is not the case. On an excursion in 1907, I visited the exact spot where I later found *Hydrocotyle vulgaris* and I can maintain with certainty that *Hydrocotyle* was not growing there at that time. The plant has, therefore, been introduced into the locality in question since that date. My opinion, therefore, that *Hydrocotyle* has immigrated by leaps and bounds directly from Denmark into Norway, is only strengthened by this discovery.

Stellaria Holostea grows along the coast from Grimstad to Bergen. It is found in Sweden from Skaane to Bohuslän, but must have migrated into southern Norway from Denmark, where it is common.

Teucrium scorodonia is found from Lyngör to Flekkefjord. In Sweden it has probably only become wild, but in Denmark it is common.

Vicia cassubica is found from Kragerö to Kristianssand. In Sweden it is found from Skaane to Dalsland, but it is common in Denmark.

Vicia lathyroides grows along the coast from the Hvaler Islands farthest east off Norway, to Kristianssand. In Sweden, however, its distribution is easterly from Skaane to Upland, so it must be assumed that it migrated into Norway directly from Jutland in Denmark, where it is not uncommon.

It will be noticed that most of these plants which I assume to have immigrated directly from Denmark (Jutland) to the south of Norway, are either bog or leguminous plants, or are such as have small seeds or stone-fruits. The carriage across water surfaces of such plants as these one would imagine could most easily take place through chance transport by birds. The distance across the Skagerak from Denmark to Norway is about 93 miles, and according to J. A. Palmén ('76) there are regular lines followed by birds of passage from Jutland to Jaederen, as also one almost to Kristianssand and another to Risör, the very places which appear to be the center of the distribution of the majority of the above-named species which I assume to have come directly from Denmark.

It is still less probable that a number of plants that belong to the coast flora of Western Europe, and in Norway are found only in the extreme west, where the winter temperature is unusually mild (from +1 to +2°C.), should have immigrated from England via Denmark and Sweden, where they do not now grow, or at any rate grow only in the extreme south. If they did make such a journey, the climate must have been so much milder in the southeast of Norway that the warm period that is proved in the Stone Age would not have gone nearly far enough. A climatic change as violent

as this would have been, and that in a comparatively very recent geological period, is not probable, nor is it necessary to assume it in order to explain the occurrence of these plants in the west of Norway, if only one does not blindly adhere to the dogma that plants can migrate only step by step.

As instances of plants which I assume have migrated from England direct to the west of Norway, the following may be mentioned:

Asplenium Adiantum nigrum is rare from Jaederen to Kristianssund. It is found in England, but only in the very east of Denmark and the extreme south of Sweden; immigration from the two last-mentioned countries seems, therefore, to be out of the question.

Asplenium marinum grows in the west of Norway from Mosterö to Stadt. It is found in England, but neither in Sweden nor Denmark.

Erica cinerea grows on the outermost islands from Farsund to Söndmöre. It is found in England, but in neither Sweden nor Denmark.

Hymenophyllum peltatum grows in the outermost coast districts from Farsund to Nordfjord. It is found in England, but neither in Sweden nor Denmark.

Scilla verna grows in the extreme coast regions from Söndfjord to Söndmöre. It is found in England, but neither in Sweden nor Denmark.

Scolopendrium vulgare is found in two or three places between Hardanger and Söndfjord. It is common in England, but it is doubtful whether it has grown in Denmark, and in Sweden it is found only in the extreme east, in Gothland.

Vicia Orobus grows farthest west, from Lister and Jaederen to Söndmöre. It is common in England, but is not found in Sweden, and only here and there in Jutland. It might thus be supposed to have come from Denmark direct to Norway, but in that case it would probably grow a little farther south than it does. I consider it, therefore, most probable that it came over from England to the coast of Norway, and then spread

along the coast southward and northward to its present limits.

It also appears, according to I. Hagen ('12), that the case is similar with regard to a number of mosses, a direct migration from England to Norway being assumed. Hagen has so little faith, however, in the ability of these plants to migrate by leaps and bounds, that he supposes a post-glacial land connection with England, over which migration might gradually take place.

This land bridge between Norway and England was originally hypothetically constructed for the pre-glacial times by L. Stejneger ('07), who considers it necessary on zoögeographical grounds. At the conclusion of his paper he says:

"I think I may safely claim to have made it appear probable:

"1. That if the characteristic and important portion of the animals and plants of west Norway, called the 'Atlantic' biota, invaded that country from Scotland, it came by way of a land bridge connecting northern Scotland with western Norway north of 59° north latitude.

"2. That this land bridge existed after the first (Scandinavian) great glaciation.

"3. That part of this biota surely survived the second (Scandinavian) glaciation along the west coast of Norway, and that possibly the climate was not too severe for all to survive.

"4. That there is a possibility of a reëstablishment of the land bridge during the 'Upper Forestian' stage with its congenial, more continental climate, during which the tenderer species may have immigrated, in case it should be proven that they could not have come with the hardier ones."

As will appear from the foregoing pages, I have also maintained ('05) that during the Last Glacial Period there was a stretch of coast in Norway that was free from ice, where some arctic plants, and, of course, also animals, were able to survive that period.

Since then Gunnar Andersson and Selim Birger ('12) have endeavored to give to the facts that favor this view the interpretation that the entire arctic flora element must have immigrated through Sweden, and followed the receding margin of ice. I consider their arguments on this point so unconvinc-

ing, especially in view of the most recent discoveries of fossil arctic plants, and my own observations of the rock formations in the west and north of Norway, that I have come to the conclusion that this iceless strip of coast was broader than I formerly supposed, and extended to the extreme southern point of Norway. In this respect my view is thus in perfect accordance with that of Stejneger.

As to whether there was an interglacial direct land connection between England and Norway, as Stejneger assumes, I cannot express an opinion, but I do not, in any case, consider it necessary for botanical reasons, although I am inclined to believe that the assumption of Stejneger will prove to be correct. On the other hand, I consider a post-glacial land connection between England and Norway, concerning which Stejneger himself is much in doubt, to be quite out of the question. There is nothing that can be brought forward to prove that previous to the post-glacial subsidence the land lay high enough for any real land bridge between Norway and England to exist. On the other hand, there are several facts that go to show that the southern part of the North Sea has lain higher than it now does, so that even considerable portions that are now under the sea were clothed with forest. This may possibly to some extent have diminished the distance between England and Norway; but the deep Norwegian Channel outside the coast of Norway has certainly been in existence ever since the Last Glacial Period.

But a land connection is not necessary to explain why the few species of plants that Norway and England have in common, and that must be assumed to have migrated over the North Sea, were able to come over in the course of the last 7,000 years. It must not be forgotten that according to J. A. Palmén ('76) there are two lines followed by birds of passage between England and the west of Norway; and that there may also have been other chance means of transport.

All things considered, I am inclined to believe that in trying to explain the distribution of vegetable species and the paths they have followed, we shall arrive at better results by studying the ways in which they spread at the present time than

by setting up hypotheses of tremendous convulsions of nature such as elevated and depressed land connections, climatic changes from cosmic causes, the oscillatory movement of the poles, etc., which can neither be proved nor disproved, as they lie beyond the spheres in which our present knowledge has a firm foundation on which to stand.

Literature Cited

Andersson, G. ('96). Svenska vaextvaerldens historia. Stockholm, 1896.

————, ('06). Die Entwicklungsgeschichte der Skandinavischen Flora. Congres Internat. Bot., Wien, 1905, Resultats scientifiques 45–97. *f. 1–30.* 1906.

————, ('09). Swedish climate in the late Quaternary period. Sveriges Geologiska Undersökning. Aarbok **1909**: 1–88. *pl. 1–2. f. 1–11.* 1909.

————, och Birger, S. ('12). Den norrlandska florans geografiska foerdelning och invandringshistorie med saerskild haensyn till dess sydskandinaviska arter. Norrlaendskt Handbibliothek v. Upsala & Stockholm, 1912.

Areschoug, F. W. ('66). Bidrag till den skandinaviska vegetationens historia. Lunds Univ. Aarsskrift **1866**:—. 1866.

Björlykke, K. O. ('00). Glaciale plantefossiler. Naturen **1900**:—. 1900.

Blytt, A. ('76). Essay on the immigration of the Norwegian flora during alternating rainy and dry periods. Kristiania, 1876.

————, ('82). Die Theorie der Kechselnden kontinentalen und insularen Klimate. Bot. Jahrb. **2**: 1–50. 1882.

————, ('82). Nachtrag zu der Abhandlung: Die Theorie der wechselnden kontinentalen und insularen Klimate. *Ibid.* **2**: 177–184. *pl. 1.* 1882.

————, ('83). Om vexellagring og dens mulige betydning for tidsregningen i geologien og laeren om arternes forandringer. Videnskabsselskabets Forhandlinger **1883**[9]: 1–31. *f. 1–2.* 1883.

————, ('06). Haandbog i Norges Flora. Udgivet ved Ove Dahl. Kristiania, 1906.

Brögger, W. C. ('00). Om de senglaciale og postglaciale nivaaforandringer i Kristianiafeltet (molluskfaunan). Norges geologiske undersögelse **31**:—. 1900–1901.

————, ('05). Strandliniens beliggenhed under stenalderen. I. Det sydoestlige Norge. Norges geologiske undersögelse **41**: —. Kristiania, 1905.

Danielsen, D. ('09). Glacialgeologiske undersökelser omkring Kristianssand. Nyt Mag. **47**: 23–95. *pl. 1–4.* 1909.

————, ('12). Kvartaergeologiske streiftog paa Soerlandet. Nyt Mag. **50**: 263–382. *pl. 7–9.* 1912.

de Geer, G. ('08). On late Quaternary time and climate. Geologiska föreningen i Stockholm foerhandlingar. **30**:—. 1908.

————, ('10). A thermographical record of the late Quaternary climate. Die Veränderung des Klimas. Stockholm. 1910.

Hagen, I. ('12). Geografiske grupper blandt Norges loevmosser. Naturen Aarg. **36**:—. 1912.

Hansen, A. M. ('04). Hvorledes har Norge faaet sit Plantedaekke. Naturen **1904**:—. 1904.

————, ('04a). Landnaam i Norge. En Utsigt over Bosaetningens Historie. Kristiania, 1904.

————, ('13). Fra istiderne. Soerlandet. Videnskabsselskabets Skrifter. I. Math.- nat. Kl. **1913**[2]:—. 1913.

Helland, A. ('12). Traegraenser og Sommervarmen. Tidsskrift for Skogbruk. Aarg. **20**:—. 1912.

Holmboe, J. ('00). Nogle ugraesplanters indvandring i Norge. Nyt Mag. **38**: 129–262. *f. 1–3.* 1900.

————, ('03). Planterester i Norske torvmyrer. Et bidrag til den norske vegetations historie efter den sidste istid. Videnskabsselskabets Skrifter. I. Math.- nat. Kl. **1903**[2]:—. 1903.

————, ('05). Studier over norske planters historie. II. Nyt Mag. **43**:33–60. 1905.

————, ('06. *Ibid.* III. *Ibid.* **44**:61–74. 1906.

————, ('09). Boegeskogen ved Lygrefjord i Nordhordland. Bergens Mus. Aarbog **1908**[18]:—. 1909.

————, ('13). Kristtornen i Norge. En plantegeografisk undersoekelse. *Ibid.* **1913**[7]:—. 1913.

Kolderup, C. F. ('08). Bergensfeltet og tilstoedende trakter i senglacial og postglacial tid. Bergens Mus. Aarbog **1907**[14]: 1–266. *pl. 1. f. 1–38.* 1908.

Nathorst, A. G. ('71). Om naagra arktiska vaextlemningar i en soettvattenslera vid Alnarp i Skaane. Lunds Univ. Ars-skrift **1870**: —. 1871.

Oeyen, P. A. ('04). Dryas octopetala L. og Salix reticulata i vort land foer indsjoeperioden. Videnskabsselskabets Forhandlinger **1904**[1]: 1–6. 1904.

————, ('07). Skjaelbanke-studier i Kristiania omegn. Nyt Mag. **45**:27–67. *f. 1–3.* 1907.

Palmén, J. A. ('76). Ueber die Zugstrassen der Vögel. Leipzig, 1876.

Rekstad, J. ('05). Jagttagelser fra terrasser og strandlinjer i det vestlige Norge. I. Bergens Mus. Aarbog **1905**[2]:1–46. *pl. 1. f. 1–12.* 1905.

————, ('06). *Ibid.* II. *Ibid.* **1906**[1]:1–48. *pl. 1. f. 1–19.* 1906.

————, ('07). *Ibid.* III. *Ibid.* **1907**[9]:1–32. *pl. 1. f. 1–15.* 1907.

————, ('08). Bidrag til kvartaertidens historie for Nordmör. 1908.

Sernander, R. ('01). Den skandinaviska vegetationens spridningsbiologi 1–459. *f. 1–32.* Upsala, 1901.

————, ('10). Die schwedischen Torfmoore als Zeugen postglazialer Klimaschwankungen. Die Verändr. des Klimas. Stockholm, 1910.

Stejneger, L. ('07). The origin of the so-called Atlantic animals and plants of western Norway. Smithsonian Misc. Coll. **48**: 458–514. *pl. 67–70. f. 1–2.* 1907.

Wille, N. ('05). Om Indvandringen af det arktiske Floraelement til Norge. Nyt Mag. **43**:315–338. 1905.

————, und Holmboe, J. ('03). Dryas octopetala bei Langesund. Eine glaciale Pseudorelikte. Nyt Mag. **41**:27–43. 1903.